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Interactive Role of Stresses on Structure and Function in Aquatic Plants

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I. Introduction

Any environmental parameter that reduces plant growth can be termed a stress factor. In most natural environments, regardless of their productivity, plants probably do not attain maximum potential growth and therefore must be considered stressed. Stress and plant productivity are interrelated such that as one stress (e.g., water stress) is ameliorated and productivity increases, other stresses (e.g., shading) increase. In general, low-productivity (oligotrophic) environments are dominated by abiotic stresses, whereas in high-productivity (eutrophic) environments, biotic stresses dominate.

This chapter examines how stresses interact to affect the growth forms, physiology, and productivity of aquatic macrophytes in oligotrophic and eutrophic environments. These two environments were selected because they represent the extremes along a gradient of productivity. The focus is first to identify the environmental factors that are most stressful in these two habitats and then to examine how these stresses affect plant structure and function over differing time scales of exposure. These considerations can help predict how multiple stresses have interacted to influence evolutionary change in structure and function and how future changes in stresses may alter community composition.

II. Stresses in the Aquatic Environment

Aquatic habitats include freshwater seasonal pools, marshes, rivers, and lakes as well as saline environments such as interior salt lakes, estuaries, and tidal and marine areas (Sculthorpe, 1967). Both microscopic and macroscopic plants live within these habitats. Macrophytes come in a variety of growth forms, including free-floating plants (e.g., duckweed, *Lemma*) and rooted plants whose foliage emerges from the water, floats on the surface, or is entirely submerged.

Stresses faced by submerged aquatic plants in freshwater lakes include (1) limited availability of inorganic carbon; (2) limited availability of other nutrients, e.g., nitrogen and phosphorus; (3) photosynthetic inhibition due to elevated oxygen levels; (4) limited light availability; and (5) microsite instability.

For several reasons, aquatic concentrations of inorganic carbon, although usually higher than atmospheric concentrations, are often limiting to photosynthesis: carbon dioxide is not readily soluble in water (particularly at higher temperatures), its rate of diffusion in water is 10^4 times slower than in air, and not all forms of inorganic carbon (e.g., bicarbonate) are used by all aquatic plants (Raven, 1970; Wetzel and Grace, 1983).

Other nutrients, in particular nitrogen and phosphorous, may limit growth. All rooted aquatic plants obtain these nutrients from the sediment; some species may also obtain nutrients from the water by means of foliar absorption (Hutchinson, 1975; Raven, 1981).

For submerged aquatic macrophytes, it is unlikely that too little oxygen would inhibit respiratory processes because oxygen is produced during photosynthesis. Moreover, because of its low solubility in water and water's high diffusive resistance, oxygen tends to accumulate in intercellular spaces within photosynthetic tissues, from which it diffuses freely to nonphotosynthetic tissues such as roots (Raven *et al.*, 1988). When photosynthesis is rapid, however, elevated oxygen levels in photosynthetic tissues may inhibit

photosynthesis via effects on photorespiration (Hough, 1974; Samishi, 1975).

Light levels are potentially limiting to the growth of aquatic macrophytes (Kirk, 1983). Water absorbs light in increasing amounts with greater depth and as turbidity from organic and inorganic suspended particles increases. In addition, because water is buoyant, aquatic macrophytes may produce structures with relatively little support, and thus the specific weight of foliage (surface area to dry weight) is typically high. Rapid growth can produce dense mats of vegetation that block out much of the light for plants beneath (Westlake, 1967; Van *et al.*, 1976).

Some stress factors are unrelated to site productivity. Aquatic environments may be stressful because the water is turbulent and the site is unstable or because the sediment is too shallow or poorly consolidated for adequate anchorage. Some sites may be unstable because of shifting sediments, which could potentially bury some plants (Hutchinson, 1975).

The importance of particular stress factors differs between oligotrophic and eutrophic lakes (Table I). Oligotrophic lakes are typically, although not always, acidic, soft-water lakes with low conductivity. Inorganic carbon, as well as other inorganic nutrients such as nitrogen and phosphorous, is low. These abiotic stresses account for the very low biomasses characteristic of oligotrophic sites. Eutrophic lakes are commonly basic, hard-water lakes with high conductivity and high levels of most inorganic nutrients. Biomass is very high, and thus the potential for competitive interference, or biotic stress, is also high.

Numerous studies have attempted to relate the trophic status of lakes, certain water chemistry characteristics, or both with species distributions (e.g., Moyle, 1945; Sculthorpe, 1967; Seddon, 1972; Hutchinson, 1975; Hellquist, 1980). Macrophytes typically cited as indicators of oligotrophic environments include species of the genus *Isoetes* (Isoetaceae), which has hundreds of species worldwide, and *Lobelia dortmanna* L. (Campanulaceae). Other macrophytes commonly found under oligotrophic conditions include species of *Littorella* (Plantaginaceae) and *Eriocaulon* (Eriocaulaceae).

Table I Comparison of Oligotrophic and Eutrophic Lakes[a]

Parameter	Oligotrophic	Eutrophic
pH	5–7	7–9
Inorganic carbon (mol m^{-3})	0.01–0.25	2.00–5.00
Conductivity (μmho cm^{-1})	<50	>200
Inorganic N (gm m^{-3} sediment)	1–3	10–20
Plant biomass (gm dry weight m^{-2})	0.1–50.0	200–800

[a] Summarized from the literature cited in the text.

Eutrophic indicator species include *Myriophyllum spicatum* L. (Haloraga-ceae) and *Potamogeton pectinatus* L. (Potamogetonaceae), but other species in these genera, as well as *Hydrilla verticillata* Royle (Hydrocharitaceae) and *Ceratophyllum demersum* L. (Ceratophyllaceae), are also found in eutrophic habitats.

III. Effect of Stresses on Macrophyte Structure and Function

Plant responses to stress need to be viewed in the context of time. Brief exposure to stress (e.g., for seconds or minutes) may affect biochemical processes; longer exposures (e.g., weeks) may induce morphological and anatomical changes. Even longer time frames may cause localized extinction of certain species and, thus, community changes. Over evolutionary time, stresses may select for structural and physiological adaptations in some species that optimize growth in the presence of conditions that would be stressful for other species. Thus limited levels of a resource may not be stressful (i.e., potential growth is not limited) to species adapted to such conditions (see also Chapters 7, 14). Conversely, an environment in which a resource is relatively abundant could nonetheless be stressful to species adapted for very rapid growth.

This chapter contrasts the structural and functional attributes of species adapted to oligotrophic and eutrophic sites and relates these to the stresses imposed by their environments. Similar comparisons have recently been made by other authors (e.g., Bowes, 1985; Boston, 1986; Chambers, 1987; Raven *et al.*, 1988).

Table II Morphological and Anatomical Comparison of Submerged Aquatic Macrophytes from Oligotrophic and Eutrophic Lakes[a]

Plant Character	Oligotrophic	Eutrophic
Indicator species	*Isoetes* spp.	*Myriophyllum spicatum*
	Lobelia dortmanna	*Potamogeton pectinatus*
Plant height (m)	0.1–0.3	1.0–2.5
Growth form	Rosette	Caulescent
Leaves		
Shape	Mostly cylindrical	Finely dissected
Surface : volume ratio	Low	High
Air space	Extensive	Limited
Chloroplast concentration	Cells adjacent to airspaces	Epidermal cells
Cuticle	Thick–moderate	Thin
Longevity	Evergreen	Winter deciduous
Root : shoot ratio	0.5–3.5	0.1–0.4

[a] Summarized from the literature cited in the text.

Structural characteristics of species such as *L. dortmanna* and *Isoetes* spp. from oligotrophic lakes differ from those of species such as *P. pectinatus* and *M. spicatum* from eutrophic habitats (Table II). The former are small rosette-forming macrophytes (Fig. 1), whereas the latter are significantly larger caulescent macrophytes (Fig. 2). One noteworthy difference between species indigenous to these two habitats is the extensive root system typical of oligotrophic species (Raven *et al.*, 1988). Leaf structure is also quite different. Oligotrophic species have thicker, bulkier leaves that are often cutinized to various degrees, compared with the much smaller, thinner, often finely dissected and weakly cutinized leaves of eutrophic species. Oligotrophic species typically have much more internal air space, contributing to their smaller leaf surface : volume ratio. Eutrophic species have chloroplasts concentrated in the epidermal cells, whereas *L. dortmanna* and species of *Isoetes* have chloroplasts distributed throughout the leaf and often concentrated around lacunae. Oligotrophic species are commonly evergreen (but cf. Keeley *et al.*, 1983), whereas eutrophic species are usually deciduous in winter.

Physiological differences are equally pronounced (Table III). Maximum photosynthetic rates, and consequently annual productivity, are substantially higher among species of eutrophic environments (Sand-Jensen and Sondergaard, 1978; Boston, 1986). Modal differences are apparent in
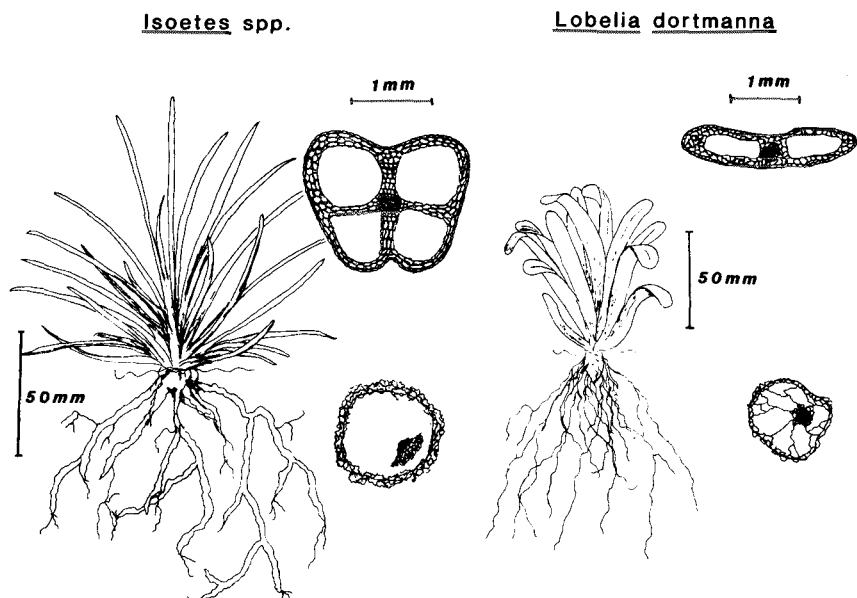

Isoetes spp.   **Lobelia dortmanna**

Figure 1 Indicator species of low-productivity oligotrophic lakes.
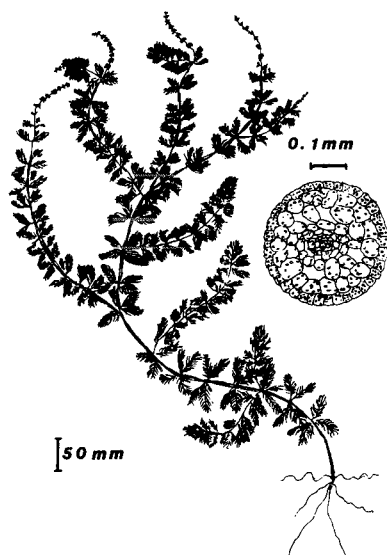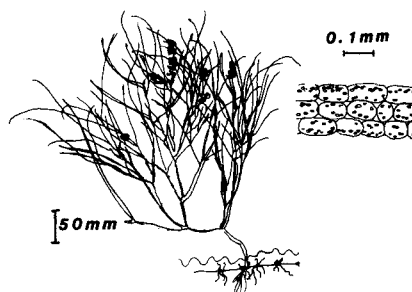
Myriophyllum spicatum   Potamogeton pectinatus

Figure 2   Indicator species of high-productivity eutrophic lakes.

mechanisms of carbon uptake and fixation. Oligotrophic species are sel-
dom capable of bicarbonate uptake, whereas eutrophic species often are
(Lucas and Berry, 1985). CAM photosynthesis is well developed in certain
oligotrophic species but absent in most eutrophic species (Keeley and
Morton, 1982); where present (e.g., *Hydrilla verticillata;* Holaday and

Table III   Physiological Comparison of Submerged Aquatic Macrophytes from Oligotrophic
and Eutrophic Lakes[a]

Plant Character	Oligotrophic	Eutrophic
Annual productivity (gm dry weight m^{-2} $year^{-1}$)	5–100	400–1000
Maximum photosynthetic rates (mg C gm^{-1} DW hr^{-1})	0.5–2.0	3–15
Bicarbonate uptake	None–little	May be substantial
CAM (dark CO_2 fixation)	Well developed in some species	Weak in some species
C_4 (light CO_2 fixation)	Weak in some species	Well developed in some species
Photorespiration	Present	Greatly reduced in some species
Carbon uptake from the sediment (% of total fixed)	40–100	<1–10

[a] Summarized from the literature cited in the text.

Bowes, 1980), it is quantitatively less important than in oligotrophic species. Fixation of carbon in the light via the C_4 enzyme PEP carboxylase is well developed in some eutrophic species (Bowes and Salvucci, 1984). Carbon uptake from the sediment is important in all oligotrophic species but quantitatively far less important in all eutrophic species (Boston *et al.*, 1987; Raven *et al.*, 1988).

IV. Structural Effects on Photosynthetic Performance

A useful model for evaluating how structure and function affect photosynthetic performance is an electrical circuit analogue of the resistances encountered by carbon dioxide along the path from the environment to the chloroplast (Nobel and Walker, 1985). For submerged aquatic macrophytes, stomatal resistance can be ignored, so the major limitations to carbon gain are the resistances of the boundary layer, cuticle, and mesophyll.

Because of the viscosity of water, boundary layers may be two to three orders of magnitude greater in submerged macrophytes than in terrestrial plants, creating a resistance that plays a dominant role in limiting carbon uptake (e.g., Black *et al.*, 1981; Raven, 1984). Although techniques are available for calculating boundary layers (e.g., Raven *et al.*, 1982), few data are available for comparing the oligotrophic and eutrophic species considered here. Several factors suggest, however, that boundary-layer effects are likely to play a greater role in oligotrophic species. These macrophytes have larger, bulkier leaves that are situated near the sediment. Eutrophic species possess thin, finely dissected foliage that is held nearer the water surface, where turbulence is greater. These considerations are complicated by differences in photosynthetic rate between oligotrophic and eutrophic species, which deplete carbon dioxide around the leaf to a different degree.

Cuticular resistance, which is closely correlated with cuticle thickness, is also greater in oligotrophic species. *Lobelia dortmanna*, for example, has a notably thick cuticle that effectively eliminates gas exchange across the leaves (Sand-Jensen and Prahl, 1982; Richardson *et al.*, 1984). *Isoetes* species and *Eriocaulon decangulare* L. also show substantial cuticular resistance (Raven *et al.*, 1988).

Several structural characteristics suggest that mesophyll resistance is also likely to be greater in oligotrophic macrophytes. The ratio of exposed mesophyll surface area to intercellular air space per unit leaf area (A^{mes}/A) is a determining factor in mesophyll resistance (Nobel, 1983). Comparative data on A^{mes}/A for aquatic macrophytes are lacking, but oligotrophic species have leaves with a lower surface : volume ratio and with relatively larger mesophyll cells than do eutrophic species such as *M. spicatum* and *P. pectinatus* (see Figures 1 and 2). One would therefore expect A^{mes}/A to be

lower in the leaves of oligotrophic species, suggesting higher mesophyll resistance in these leaves relative to those of eutrophic species.

In addition, many eutrophic macrophytes have leaves with only two or three cell layers and with chloroplasts concentrated in the epidermal layer, factors that shorten the path of carbon uptake and greatly reduce mesophyll resistance. These considerations suggest that, on the whole, leaf resistance to carbon uptake is likely to be greater in oligotrophic species.

V. Interactive Stresses, Structure, Function, and Plant Productivity

Figure 3 presents a schematic model of how stresses in oligotrophic environments may interact in affecting the functional attributes of macrophytes. Low carbon availability, coupled with low nitrogen and phosphorus availability, contributes to low photosynthetic rates and, consequently, low primary production. Low photosynthetic rates generate less oxygen, and photorespiratory inhibition by oxygen is thus likely to be lower than in eutrophic environments. Low productivity will generate less shading and minimize limits imposed by light on growth.

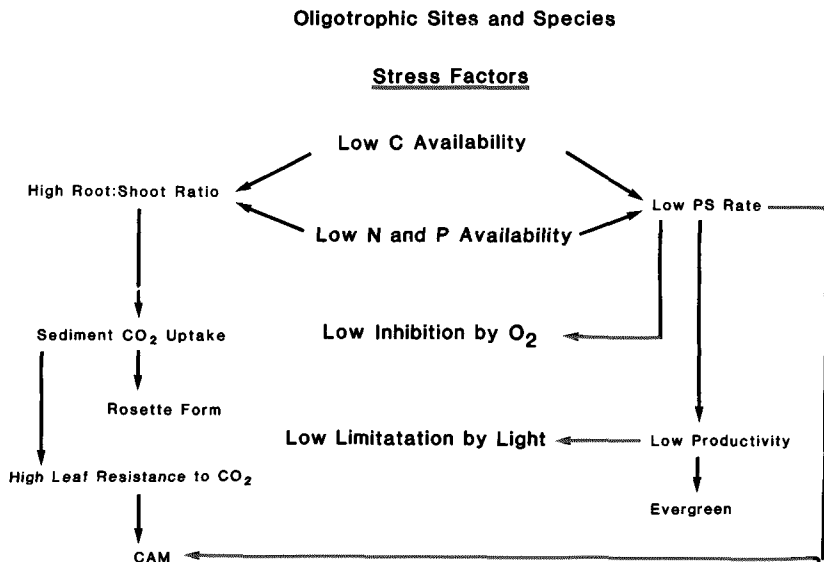Environments with severe carbon limitation might be expected to select

Figure 3 Interaction of stresses and plant structure, function, and productivity in oligotrophic lake environments. PS, photosynthesis.

for leaf structural attributes that reduce resistances to carbon uptake, a prediction not upheld for oligotrophic macrophytes (as discussed above). The explanation is simply that these species obtain much of their carbon from the sediment, a source much richer in carbon than the water column, despite its greater diffusive resistance to carbon dioxide (Raven *et al.*, 1988).

Other factors may also be involved. Bloom *et al.* (1985) suggest that "plants reduce disparity in supplies of carbon and nutrients by increasing their capacity to acquire the most limiting resource . . . [and] adjust allocation so that their growth is equally limited by all resources." In the face of severe nitrogen and phosphorus limitation, allocating more resources to root mass is to be expected in oligotrophic species. Indeed, some evidence indicates that these nutrients are more limiting to oligotrophic macrophytes than is carbon (Sand-Jensen and Sondergaard, 1979; Moeller, 1983; Boston and Adams, 1987). Such a commitment of resources to roots undoubtedly favors acquisition of carbon from the sediment. This, in turn, would select for other structural characteristics, such as the rosette growth form, which provides a short diffusion pathway from sediment to leaves, and extensive lacunal volume in both leaves and roots, which increases the diffusion of gases from roots to leaves. Under these conditions, one might expect the sediment to act as a source of carbon and the water as a sink; selection for higher cuticular resistance would thus be expected. CAM photosynthesis, which extends the diel period of carbon fixation, would be selected by low photosynthetic rates and, as leaf conductance decreases, may become more efficient, since leakage of carbon dioxide out of the leaves during decarboxylation would be minimized (Keeley *et al.*, 1983; Boston and Adams, 1987; Madsen, 1987). Characteristics such as thick leaves, large lacunal airspaces, and carbon uptake from the sediment would not be compatible with bicarbonate uptake. This incompatibility could explain why it may not be energetically advantageous for oligotrophic species to use this carbon source, even though bicarbonate can account for 25–90% of the total inorganic carbon pool in oligotrophic habitats (Hutchinson, 1975). Overall, the limitations to carbon gain in oligotropic lakes are substantial, resulting in low productivity. This factor may have been important in selection of the evergreen habit, which conserves nutrients and extends the annual period for photosynthetic production, even under winter ice cover (Boylen and Sheldon, 1976).

Submerged aquatic macrophytes indicative of eutrophic sites have responded quite differently to the largely biotic stresses of their environment (Fig. 4). Elevated levels of carbon and other inorganic nutrients allow for high photosynthetic rates. These high rates generate more oxygen and increase the potential for photorespiratory effects (Salvucci and Bowes, 1983; Holaday *et al.*, 1983). High photosynthetic rates also result in high
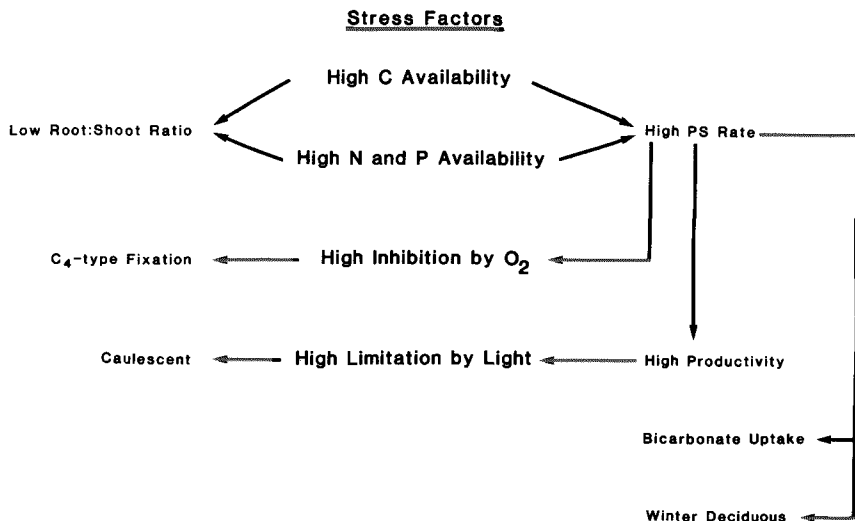
Eutrophic Sites and Species

Stress Factors

Low Root:Shoot Ratio

High C Availability

High N and P Availability

High PS Rate

C_4-type Fixation   High Inhibition by O_2

Caulescent   High Limitation by Light   High Productivity

Bicarbonate Uptake

Winter Deciduous

Figure 4   Interaction of stresses and plant structure, function, and productivity in eutrophic lake environments. PS, photosynthesis.

productivity. As biomass production (by macrophytes and microphytes) increases, the potential for shading increases, and selection for a caulescent growth form is expected (*e.g.,* Titus and Adams, 1979; Barko and Smart, 1981). High photosynthetic rates select for smaller, thinner leaves that minimize resistance to carbon uptake. Small leaves likewise reduce sedimentation and epiphyte establishment, thus reducing shading caused by those factors. High photosynthetic rates, coupled with the higher pH typical of eutrophic sites, put a premium on the ability to use alternative inorganic carbon species such as bicarbonate. Photosynthetic inhibition by high oxygen concentrations may be a major factor in selection for C_4 fixation of carbon dioxide in the light (e.g., *Hydrilla verticillata;* Holaday and Bowes, 1980); lack of this carboxylation pathway in *M. spicatum* (Salvucci and Bowes, 1983) and *P. pectinatus* (Winter, 1978), however, suggests there are other mechanisms for reducing photorespiratory effects. Low nutrient stress, coupled with selection for the caulescent habit to overcome limited light, has selected for low root:shoot ratios. High photosynthetic rates are commonly associated with high respiratory rates; this, coupled with cool temperatures and short days during winter, may have selected for the deciduous habit.

In aquatic habitats there are, of course, stress factors unrelated to productivity, such as turbulence from waves or currents and sediment

deposition. In general, the low-growing rosette of oligotrophic macrophytes may preadapt them for tolerating turbulence. Seddon (1965) noted that *Isoetes echinospora* Dur. could avoid being outcompeted in eutrophic environments only on sites where exposure to wave action prevented growth of caulescent species. The rosette growth form, however, is maladaptive on sites with rapid sedimentation (Spence, 1982).

VI. Perturbations and Predictions of Community Composition

The above considerations suggest that changes in site productivity should be accompanied by predictable changes in species composition. Eutrophication has occurred over historical times in many aquatic systems, and changes in macrophyte composition have always followed. Eutrophic enrichment with nitrogen and phosphate leads to luxuriant growth of *Myriophyllum* and *Potamogeton* species and the disappearance of oligotrophic species (Roelofs, 1983; Ozimek and Kowalczewski, 1984; Farmer and Spence, 1986). An increase in one macrophyte species could potentially change biotic stresses in the environment, and such changes may account for the cyclic or wave pattern that invasions often follow, with one invasive species replacing another (Carpenter 1980). As pollution intensifies and a system becomes hypereutrophic, the availability of nutrients increases selection for species with minimal resistance to carbon uptake; the resulting phytoplankton "blooms" pose a severe light stress for rooted macrophytes. Changes such as these (Fig. 5) have been documented for the natural
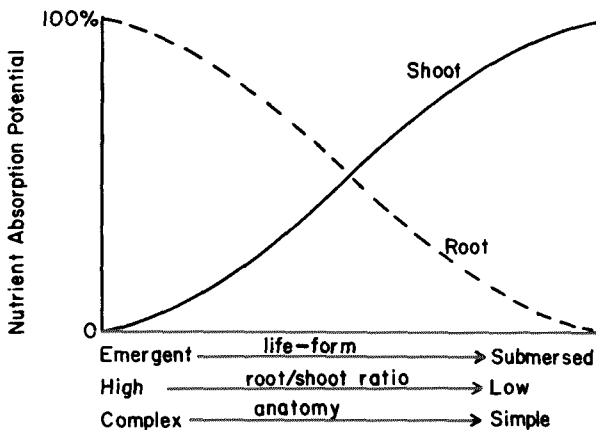

Figure 5 Hypothetical changes in the relative primary productivity of submerged, emergent, epiphytic, and planktonic communities as nutrient enrichment increases. [Reprinted from Davis and Brinson (1980).]

community succession that occurs in systems that are gradually becoming fertile (Wilson, 1935).

Acidification of lakes is now a significant factor affecting site productivity. The drop in pH caused by sulfuric-acid precipitation acidifies the water column and releases carbon dioxide from the water (Dillon *et al.,* 1987); these effects are most evident in poorly buffered oligotrophic habitats. The effect on the water column is to decrease the concentration of inorganic carbon. If the substrate is high in inorganic carbon, acidification of the overlying water column may increase the concentration of carbon dioxide in the sediment. Other effects include increased sulfate concentration; decreased nitrification, and thus higher ammonium concentration; and decreased microbial turnover of organic matter (Roelofs, 1983). These changes exacerbate the stress of low nutrient availability so much that isoetid species such as *Lobelia dortmanna* and *Isoetes* spp. disappear, resulting in an overall drop in macrophyte production and diversity (Roelofs, 1983; Schuurkes *et al.,* 1986).

The future effects of rising carbon dioxide levels in the atmospheric are open to speculation (Wetzel and Grace, 1983). In eutrophic habitats, the relative increase in carbon dioxide will be small, whereas in oligotrophic habitats, it will potentially be significant. Plants in these oligotrophic environments are likely to respond with increased photosynthetic rates, but this change would be transitory. For as primary production increases, other nutrients would become tied up in biomass, thus limiting productivity.

VII. Conclusions

Responses to stress described here for aquatic macrophytes have parallels for terrestrial systems. Abiotic stresses in oligotrophic aquatic environments have selected for a markedly different suite of plant traits from those selected for by the biotic stresses dominating eutrophic environments. Abiotically stressful terrestrial environments such as deserts are often dominated by species with high root : shoot ratios, a rosette growth form, and well-cutinized, evergreen leaves, and many such species have CAM photosynthesis (Chapter 14), all characteristics of abiotically stressful aquatic habitats as well. Highly productive terrestrial habitats are dominated by biotic stresses. Low root : shoot ratios, C_4 photosynthesis and the caulescent growth form are examples of characteristics held in common with aquatic species. Thus, the responses to stress are more closely tied to the form of the stress, biotic or abiotic, than whether it occurs on land or in the water.

Acknowledgments

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1991